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Absorption and Translocation of Sodium in Beans and Cotton[1]

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Summary. At the end of a 4 hour absorption period approximately 95 % of the sodium absorbed by bean plants was retained in the secondary roots. The sodium translocated to the shoot was retained in the stem.

2,4-Dinitrophenol decreased the amount retained in the secondary roots of bean plants and increased the amount translocated to the shoot. The stem retained most of the translocated sodium.

Bean plants without roots absorbed considerably more sodium than plants with roots and translocated a greater proportion of the sodium to the petioles and blades. 2,4-Dinitrophenol reduced the amount of sodium in the stem and petioles and increased the amount in the blades.

2,4-Dinitrophenol reduced the amount of sodium retained by the secondary roots of cotton plants but did not appreciably affect the amounts translocated to the shoot.

The amount of sodium that plants absorb and translocate to the shoot varies according to the species. Among 21 species grown on culture solutions containing equivalent amounts of sodium, potassium, and rubidium, Collander (6) found a wider range in the amount of sodium absorbed than in the amount of either potassium or rubidium absorbed. Other studies have indicated that bean (8, 23), soybean and corn (13, 14), and deciduous fruit and nut trees (1, 4, 11) translocated very little sodium to the shoot, whereas beets (2, 3, 19) and cotton (5) readily translocated sodium to the shoot.

Bower and Wadleigh (3), using sand-resin mixtures adjusted to several levels of exchangeable sodium, and Lagerwerff and Holland (17), using culture solutions adjusted to 3 sodium-adsorption-ratios and 3 total-salt concentrations, found that sodium was translocated to the top of bean plants but only in the presence of high sodium concentrations in the medium. Jacoby (16) and Pearson (22) found that bean plants normally retained sodium in the basal portions of the stem but that sodium translocation was increased at higher external concentrations.

Sodium translocation to bean shoots was also increased by 2,4-dinitrophenol (DNP) (22). The translocation of sodium to the shoots of barley, snapdragons, and bluegrass was increased by anaerobic conditions (18, 20, 21). Thus, the restriction of sodium transport to the shoot of some species appears to be regulated, at least in part, by metabolism.

With respect to beans, the increased translocation of sodium to the shoot at high external concentrations or in the presence of an inhibitor might be anticipated if it is assumed that there is a reciprocal relationship between the amount of sodium retained in the root and the amount translocated to the shoot. If such a reciprocal relationship existed, sodium translocation to the shoot should be increased in the presence of a metabolic inhibitor as a result of decreased accumulation in the root. If it is assumed that roots have a strong affinity but a relatively small capacity for sodium, translocation to the shoot should be increased as the roots approach saturation with sodium.

Gauch and Wadleigh (9) proposed that sodium translocation in beans may be regulated by a membrane that prevents the passage of sodium into the vascular tissue in the root. The effectiveness of such a membrane could be reduced in the presence of a metabolic inhibitor allowing sodium to leak into the vascular stream, thereby increasing the amount of sodium translocated to the shoot. Ginsburg (10) reported that DNP induced the leakage of red pigment out of beet root slices and attributed this leakage to an effect of DNP on the structure of the semipermeable membranes.

Based on the sodium distribution in the leaves, twigs, branches, and trunks of deciduous fruit and nut trees, Bernstein et al. (1) proposed that sodium translocation may also be regulated by withdrawal

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from the vascular stream into the living cells adjacent to the vascular tissue. Such a withdrawal mechanism could be related to metabolism and, therefore, altered in the presence of DNP.

The regulation of sodium movement in bean plants could involve both of these latter mechanisms. A membrane or series of membranes in the root could regulate the entry or leakage of absorbed sodium into the vascular stream. Sodium that entered the stream could subsequently be withdrawn by the living cells adjacent to the vascular tissue.

Experiments have been conducted to determine the effect of time and several concentrations of DNP on the absorption and translocation of sodium in bean and cotton plants. These plants were selected because they are morphologically similar but differ in their ability to translocate sodium. Additional experiments were conducted to investigate in detail the retention of sodium in the stem tissue of bean plants without roots.

Materials and Methods

Red kidney bean (*Phaseolus vulgaris,* L.) and Arizona 124-68 cotton (*Gossypium hirsutum* L.) seeds were germinated in sand which was flushed every 30 minutes with a 0.1 dilution of Hoagland's No. 1 nutrient solution, while the micronutrients (except iron) were supplied at full strength (12). Iron was supplied as Fe-EDTA at a concentration of 5 mg/l (15).

Approximately 5 days after emergence, single seedlings were transferred to 14-liter crocks which contained the same dilute culture solution used during germination. The bean and cotton plants selected for treatment were as uniform as possible and had developed at least 3 trifoliolate leaves or 6 true leaves, respectively. Plants of this size were approximately 2 to 3 weeks old. Axillary buds were removed during the growing period.

Absorption took place from polyethylene vessels containing 800 ml of aerated solution. The plant holder also served as a lid and was sufficiently large to cover the absorption vessel completely, thereby minimizing solution losses by evaporation.

The composition of the absorption solution in mmoles/l was: tris, 5.0; $CaCl_2$, 0.5; plus an appropriate amount of NaCl labeled with 5 μc ^{22}NaCl. Calcium was included in the absorption solution to maintain the integrity of the selective absorption mechanism (7). All solutions were adjusted to pH 6.5 with HCl. In experiments involving inhibitors, the plants were pre-conditioned for 1 hour, using a solution containing buffer, $CaCl_2$, and inhibitor. This was done to enable the inhibitor to block the metabolic steps or alter the permeability of membranes involved before the plant was exposed to sodium.

During the pre-conditioning and absorption periods, the plants were placed under a bank of 8 cool-white fluorescent tubes and 5 60-watt incandescent bulbs in the greenhouse. This assured a light intensity of at least 2000 ft-c at plant height.

At the end of the absorption period, surface-film and free-space ^{22}Na was removed from the roots by repeatedly immersing them for 2 minutes into a solution containing buffer, $CaCl_2$, and ^{23}NaCl (50 meq/l). A preliminary experiment indicated that there was very little increase in the amount of sodium desorbed after the first minute. In order to minimize the carryover of solution in transferring roots from 1 solution to another, the roots were allowed to drain freely for exactly 1 minute before transfer.

After desorption, the plant material was separated into root and shoot by severing the secondary roots at their point of origin on the main axis. The lower hypocotyl, which was directly exposed to the absorption solution, was included with the shoot. During desorption, it was repeatedly submerged in the desorption solution. With respect to sodium accumulation, the lower hypocotyl resembled the upper hypocotyl more than it did the secondary roots. For the detailed examination of the sodium content of the various parts of the plant, the petioles and blades were removed individually, and the stem was cut at each node. The sodium content was then determined for each separate stem section, petiole, and blade.

The ^{22}Na content of the plant samples was measured with a scintillation well-counter having an efficiency of approximately 40 %. The ^{23}Na content of the plant material was then calculated from the ^{22}Na measurements of the samples and the ^{22}Na/^{23}Na ratio of the absorption solution.

Results

The first experiment was designed to study the effect of the sodium concentration in the external solution on the absorption and translocation of sodium within the plant. The solution concentrations used were 0.3, 1.0, 3.0, 10.0 and 30.0 meq NaCl/l. The absorption period was 4 hours. One bean or cotton plant was selected for each concentration. The amounts of sodium found in the various tissues are shown in table I.

Although none of the treatments was replicated, the trends are quite clear. The total amount of sodium absorbed by both beans and cotton increased as the external concentration was increased. Some sodium was translocated to bean shoots but it was effectively retained in the stem since the petioles and blades contained virtually no sodium, even at the highest external concentration. The proportions of absorbed sodium found in the various tissues of cotton were very nearly the same at all external concentrations studied.

The sodium content of bean and cotton plants as a function of absorption time in the presence and absence of 50 μM DNP is presented in table II. The external sodium concentration was maintained constant at 10 meq/l. Treatments were unreplicated.

There was a direct relationship between the sodium

Table I. *Sodium Content of Bean and Cotton Plants as a Function of the External Sodium Concentration*
Absorption period was 4 hours.

Plant tissue	External sodium concentration (meq/l) 0.3	1.0	3.0	10.0	30.0
	μeq	μeq	μeq	μeq	[illegible]
			Bean		
Secondary root	0.5	1.9	6.5	49.0	157.4
Stem	0.1	0.3	0.5	1.7	12.2
Petiole	0.0	0.0	0.0	0.1	0.4
Blade	0.0	0.0	0.0	0.1	0.2
Total	0.6	2.2	7.0	50.9	170.2
			Cotton		
Secondary root	0.9	3.4	8.3	32.4	110.2
Stem	0.3	0.5	1.6	6.4	14.0
Petiole	0.1	0.2	0.7	2.5	6.7
Blade	0.4	1.0	2.4	15.4	43.8
Total	1.7	5.1	13.0	56.7	174.7

Table II. *Sodium Content of Bean and Cotton Plants as a Function of the Length of the Absorption Period in the Presence and Absence of DNP*
External sodium concentration was 10 meq/l.

Plant tissue	Length of absorption period (min) 15	30	60	120	240	15	30	60	120	240
			— DNP					50 μM DNP		
	μeq	μeq	μeq	μeq	μeq	μeq	μeq	μeq	μeq	μeq
					Bean					
Secondary root	12.1	22.8	62.3	69.3	158.7	11.1	15.2	41.4	65.1	127.0
Stem	0.4	0.9	2.6	2.4	6.6	1.1	2.4	6.0	10.6	28.0
Petiole	0.1	0.1	0.1	0.1	0.1	0.1	0.3	1.6	4.2	11.7
Blade	0.1	0.2	0.1	0.2	0.1	0.1	0.2	1.3	4.6	16.3
Total	12.7	24.0	65.1	72.0	165.5	12.4	18.1	50.3	84.5	183.0
					Cotton					
Secondary root	10.4	12.9	23.8	38.4	40.7	7.3	10.5	5.7	15.7	13.2
Stem	3.0	2.5	4.8	7.5	16.9	2.9	4.5	4.6	10.3	17.2
Petiole	0.6	1.2	2.7	4.3	9.4	0.8	1.2	1.5	4.5	8.2
Blade	1.7	4.9	11.6	19.5	48.7	0.6	1.2	2.3	10.7	36.7
Total	15.7	21.5	42.9	69.7	115.7	11.6	17.4	14.1	41.2	75.3

Table III. *Sodium Concentration of Bean and Cotton Plants as a Function of DNP Concentration*
External sodium concentration was 10 meq/l. Absorption time was 4 hours.

Plant tissue	DNP concentration (M) 0	5×10^{-6}	2×10^{-5}	5×10^{-5}	2×10^{-4}	5×10^{-4}
	μeq	μeq	μeq	μeq	μeq	μeq
			Bean (triplicate)			
Secondary root	141.1	85.8	93.0	69.7	83.4	65.7
Stem	7.2	11.0	17.1	18.1	24.2	25.6
Petioles	0.0	0.1	1.4	4.0	4.2	4.5
Blades	0.0	0.1	0.5	4.2	2.8	4.4
Total	148.3	97.0	112.0	96.0	114.6	100.2
			Cotton (duplicate)			
Secondary root	77.2	35.5	45.8	24.5	49.8	46.9
Stem	20.4	7.4	15.3	21.4	18.2	20.4
Petioles	6.4	4.8	8.8	8.4	6.4	6.4
Blades	17.0	9.5	20.4	13.8	19.6	19.8
Total	121.0	57.2	90.3	68.1	94.0	93.5

content of the plants and the length of the absorption period in either the presence or absence of DNP. The amount of sodium in bean roots or cotton roots and shoots was decreased in the presence of DNP. However, the amount of sodium in bean shoots was considerably increased by DNP. The increase in the amount of sodium in the shoots more than offset the decrease in the roots of bean plants at the 2 longer time intervals.

The sodium content of bean and cotton plants exposed to several concentrations of DNP is shown in table III. The external sodium concentration was 10 meq/l and the absorption time was 4 hours. The data are averages for 3 bean plants or 2 cotton plants at each DNP concentration.

All concentrations of DNP reduced the sodium content of cotton roots or shoots and bean roots. The sodium content of bean shoots increased progressively as the DNP concentration was increased in the absorption solution. However, unlike cotton, the sodium content of the bean blades was essentially the same as the content of the petioles and both tissues contained considerably less sodium than the stems. Thus, even though sodium translocation in beans was enhanced by DNP there was no evidence of a surge to the leaves.

The amount of sodium within the stem sections of bean plants decreased progressively with increasing distance from the root (fig 1). Even though more sodium was translocated to the shoot of bean plants treated with DNP the same pattern of sodium distribution within the stem was noted. This suggests that sodium may have been withdrawn from the transpiration stream by the living cells adjacent to the vascular tissue. DNP had no apparent effect on the distribution of sodium in cotton stems.

The influence of DNP on the withdrawal of sodium from the vascular stream of bean plants was studied in plants from which the roots had been removed. It is to be noted that the removal of the roots increased the sodium content of the stems, petioles and blades (table IV). DNP reduced the amount of

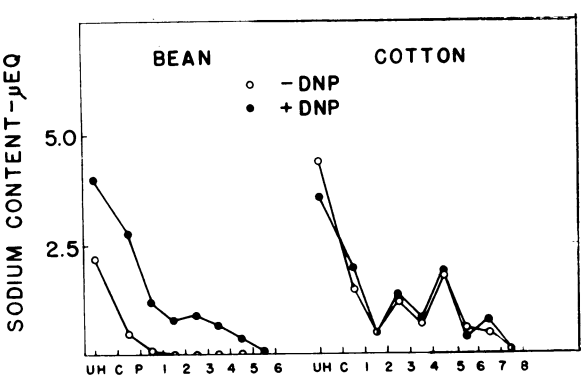

FIG. 1. The sodium content (μeq) of bean and cotton internodal stem sections. UH, C and P refer to upper hypocotyl, cotyledonary and primary nodes, respectively. Numbers refer to nodal connections for true leaves.

Table IV. *Sodium Content of Bean Plants Without Roots in the Presence and Absence of DNP*

External sodium concentration was 10 meq/l. Absorption time was 4 hours. The DNP concentration was 50 μM.

Each value is the average of triplicate cultures.

DNP	Stem	Petiole	Blade	Total
	μeq	μeq	μeq	μeq
—	170.6	90.8	157.8	419.2
+	81.7	52.4	210.4	344.5

sodium retained in the stems and petioles and increased the amount translocated to the blades.

The sodium content of the stem sections, petioles and blades is shown in figure 2. Again the amount in the stem decreased with increasing distance from the base of the plant but the amount in the petioles and blades increased to a maximum in the vicinity of the apex of the plant.

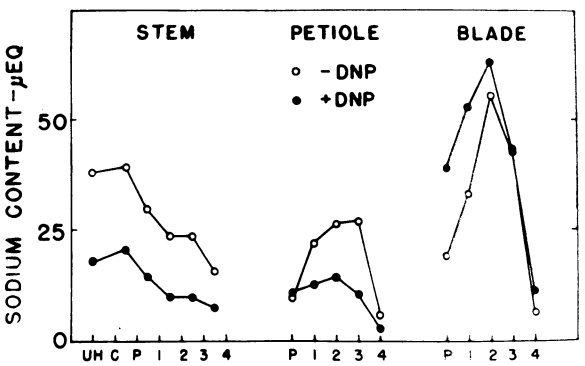

FIG. 2. The sodium content (μeq) of bean internodal stem sections, petioles and blades. UH, C and P refer to upper hypocotyl, cotyledonary and primary nodes, respectively. Numbers refer to nodal connections for true leaves.

Discussion

In the present study it has been shown that DNP reduced the amount of sodium retained in bean roots and increased the amount translocated to the shoot. However, within the shoot of intact plants treated with DNP, the stem still contained more sodium than either the petioles or blades, and the sodium content within the stem sections progressively decreased with increasing distance from the root.

When much greater amounts of sodium entered the bean shoot (plants without roots), a larger proportion of the sodium was found in the blades. Under these conditions it was also noted that DNP reduced the amount in the stem and increased the amount in the blades. However, the relative distribution of sodium within the stem was unaffected by DNP or the total amount of sodium present in the shoot.

The increased sodium translocation to the shoot of bean plants treated with DNP supports the pro-

posal (9) that sodium is retained in bean roots by a membrane system. The efficiency of this system was reduced by DNP.

When relatively low amounts of sodium are translocated to bean shoots very little passes through the stem into the petioles and blades. However, when large amounts of sodium are translocated to bean shoots, more than half of the sodium passes through the stem into the petioles and blades. The proportion retained by the stem tissue was markedly reduced by DNP.

Thus, it appears that bean roots are capable of retaining large amounts of sodium and bean stems are capable of retaining the small amounts of sodium translocated to the shoot. Both of these mechanisms are sensitive to DNP. However, the effect of DNP on the retention mechanism in the stem was noted only when large amounts of sodium were present in the shoot.

DNP reduced the amount of sodium retained by cotton roots, but had no apparent effect on the distribution of sodium in cotton shoots.

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